Sediment Trap Studies in Southeastern Lake Michigan: Fecal Pellet Express or the More Traveled Route?

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ABSTRACT. *This study investigated the composition of particulate matter in a series of sediment traps set in the offshore waters of southeastern Lake Michigan, April to October 1982. Of particular interest was the role of zooplankton fecal pellets in rapidly transporting matter from the euphotic zone to lake sediments. Particulate flux was examined microscopically. Dry weight and settling velocities were then estimated based on literature conversion factors and predictive equations. There was an excellent correspondence between estimated flux and direct measurements of flux. Flux was dominated by biological particles of autochthonous origin: fecal matter, fecal pellets, organic aggregates, phytoplankton, and zooplankton exoskeletons. Particles were small with slow (generally < 10 m/day) settling velocities. Flux varied seasonally, being highest in spring and autumn, during vertical mixing, and lowest in mid-summer, during strong thermal stratification. High trapping rates during isothermal conditions previously have been associated with resuspension. However, free minerals were a relatively small component of flux. This suggests that isothermal events are associated with the resuspension of previously-settled mineral particles with these particles and slowly-settling biological particles being kept in suspension until the onset of thermal stratification. Because zooplankton fecal pellets and fecal matter are subject to significant degradation and reingestion during the days to weeks that are required for them to reach the lake floor, these egestion products may play a greater role in the recycling of matter in the water column than in the direct transport of matter to the sediments. During summer, when the abundant zooplankton population is food-limited and cladocerans, which produce diffuse egestion products are numerous, relatively little of materials produced in the epilimnion settles immediately to the lake floor.*

INDEX WORDS: Fecal pellets, sediment traps, organic aggregates, resuspension, recycling, Lake Michigan.

INTRODUCTION

In recent decades, interest has grown in the processes by which matter is lost from the euphotic zone to the sediments. Such matter includes organic carbon, nitrogen, and biogenic silica (Bishop and Marra 1984, Eadie *et al.* 1984, Gardner *et al.* 1989), toxic organics (Elder and Fowler 1977, Prahl and Carpenter 1979, Baker *et al.* 1991), and various minerals and metals (Higgo *et al.* 1977, Honjo *et al.*

1982, Robbins and Eadie 1991). While small particles dominate in marine and fresh waters, such particles have relatively small settling velocities (McCave 1975, Chase 1979). Rather, it is the rarer, larger particles with their greater settling velocities which provide for the major sedimentation of matter through the water column. In offshore oceanic waters, zooplankton fecal pellets and fecal matter have been implicated as providing the major transport pathway of matter to greater ocean depths (Bishop *et al.* 1977, Elder and Fowler 1977, Higgo *et al.*

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1977). In many regions, seasonal variations in flux are closely tied with the annual cycle of primary productivity (Deuser *et al.* 1981, Honjo 1982).

Particulate flux processes are considerably more complex in coastal waters and in estuaries. For example, terrestrial inputs may be large, especially during periods of strong runoff (Ansell 1974, Webster *et al.* 1975). However, even in regions where terrestrial inputs of matter are significant, zooplankton fecal pellets may have a major role in the downward transport of matter (Taguchi and Hargrave 1978, Prahl and Carpenter 1979). Resuspension is another important process affecting particulate flux in shallow, marine waters. During some seasons, sediments serve both as a source of particulate flux and as a transport pathway (Oviatt and Nixon 1975, Hargrave and Taguchi 1978).

Particulate flux studies conducted in lakes ranging in size from a few hectares to the Great Lakes have shown that terrestrial and littoral zone inputs, resuspension, and lateral transport are all important processes affecting the sedimentation of matter (Eadie *et al.* 1989, Schelske *et al.* 1984, Rosa 1985, Robbins and Eadie 1991). However, relatively little is known about the physical components of particulate flux, including zooplankton fecal pellets, in the downward transport of matter in limnological environments.

It is possible that the role of zooplankton in particulate flux varies between marine and fresh waters. Freshwater zooplankton communities are dominated by microzooplankton. Macrozooplankton such as mysids generally are a minor component of freshwater zooplankton communities, especially during daylight hours. In contrast, marine systems support an abundant macrozooplankton assemblage including calanoid copepods, euphausids, and mysids all of which produce large, well-packaged fecal pellets. Cladocerans are a major component of summer-autumn freshwater communities, particularly mesotrophic and eutrophic communities. Such zooplankton do not produce discrete fecal pellets but rather diffuse egestion products. Cladocerans are minor components of most marine communities. Given these two considerations, it is possible that freshwater zooplankton play a smaller role than marine zooplankton in the sedimentation of particles from the euphotic zone to the sediments.

This manuscript is based on a seasonal study of particle flux characteristics at a 100-m deep station in southeastern Lake Michigan located approximately 30 km offshore of Grand Haven. The study,

which is based on the detailed microscopic examination of particulate flux, addresses the following questions. What are the probable sources and composition of particulate flux in the offshore waters of southeastern Lake Michigan? What are the major pathways transporting matter from the lake surface to the lake sediments? What is the probable fate of that flux? What are the similarities and differences between oceanic and lacustrine flux? What are the environmental implications of these differences?

METHODS

Field Studies

Particulate flux studies were conducted offshore of Grand Haven, Michigan in 100 m of water. Duplicate 10-cm diameter Plexiglas traps with a 5:1 height to width ratio were set at depths of 10, 20, 30, 40, 60, 80, and 95 m. Particle flux was collected in a 500-mL wide mouth bottle placed at the bottom of the trap and under a funnel. One trap was preserved with chloroform (20 mL) and the other with mercuric chloride (100 mg/L). Traps were set on 26 April 1982 and then recovered and reset at approximately one-month intervals until 27 October when the study was terminated. Analysis of pairs of traps show that the difference of material collected between pairs averages 11% (Eadie 1997). Samples collected in the mercuric chloride traps were used in the microscope study reported here. Samples were stored in the dark and in a refrigerator until analysis. Samples preserved with chloroform were freeze-dried then weighed to calculate mass flux and aliquots were analyzed for total and organic carbon and nitrogen on a CHN analyzer. These direct determinations of flux were later compared with total mass flux estimates based on the microscope techniques described below.

Microscopic Methods

Descriptions of the physical composition of flux were based on direct, microscopic observations of subsamples from each trap series. Each sample bottle was made up to 500 mL (with distilled water), the particles gently resuspended, and a subsample rapidly withdrawn using a pipette. The actual volume withdrawn depended upon the amount of particulate material contained in each sample bottle. As little as 0.02 mL (April to May) and as much as 5.0 mL (July to August) were withdrawn. The resulting subsample was gently filtered along with

about 5 mL of distilled water onto a 0.8 μm, 22-mm diameter Millipore filter. The filter was rinsed with approximately 10 mL of 50% and then 95% ethanol prior to preparing a clove oil slide (Glover 1982). Each slide was examined at 95X under a compound microscope. One half of a transect was examined per slide, providing counts of several hundred particles. Because large fecal pellets (which were of special interest to this study) were relatively rare, half a filter (representing a larger volume of subsample) was examined on several occasions to obtain more detailed data on the abundance and size of these particles.

Detailed qualitative and quantitative information was obtained during the examination of each slide. Such information was obtained for "composite" particles (fecal pellets, fecal matter, organic aggregates, and inorganic aggregates) and for "individual" particles (primarily minerals, phytoplankton, and zooplankton exoskeletons). These visual observations formed the basis for estimating total dry weight flux.

Fecal pellets had well-defined boundaries, were densely packed, and generally cylindrical in shape (Glover and Evans 1981). Fecal matter was less densely packed, had moderately well-defined boundaries, and was ellipsoidal in shape. Organic aggregates were irregular in shape and contained a loose aggregation of phytoplankton fragments, minerals, and other matter. Inorganic aggregates were similar to organic aggregates but contained a greater predominance of minerals. Separation into the four categories was subjective and, on occasion, difficult. The length and width of each composite particle was measured as it was encountered on the microscope slide.

Minerals were classified into three size categories: < 4 μm, 4–10 μm, and > 10 μm. Length and width of particles > 10 μm was determined. Minerals were further classified into light, medium, and opaque particles. Phytoplankton were identified to species and the number of cells enumerated both for single and colonial species. Phytoplankton were further classified into seven categories: live colony, dead colony, live cell, dead cell, more than half a dead cell, half a dead cell, and less than half a dead cell. Cell length and widths were not determined. Zooplankton exoskeletons also were counted but not identified: nor were dimensions determined. Intact zooplankton also were enumerated but were not included in flux calculations: it was assumed that intact zooplankton swam into the trap and thus were not a true component of flux.

Dry Weight Flux Estimates

After particles were enumerated and measured, their volume and dry weights were estimated. The volume of fecal pellets was estimated assuming that these particles were cylindrical in shape; mass calculations were based on the assumption that they had a specific gravity of 1.22 (Komar *et al.* 1981) and were 77% water. Fecal matter and organic aggregates were assumed to be ellipsoidal in shape. Fecal matter, which was less densely packed than fecal pellets, was assumed to have a specific gravity of 1.15 and to be 85% water. Research, to date, has not determined the specific gravity and wet weight to dry weight conversions of freshwater aggregates. However, Alldredge and Gotschalk (1988) determined that the density of marine snow (most of which varied in length from 2.4 to 75 mm) had a median density of 1.0249 g/cm^3. Smaller diameter (0.1 mm) particles had an estimated density of 1.0967 g/cm^3: these researchers did not estimate the density of smaller aggregates. Lake Michigan organic aggregates, which were even smaller than in Aldredge and Gotschalk's study, appeared to contain less mineral matter and diatom frustules as they increased in size. Therefore, it was assumed that aggregates < 10 μm in length had a specific gravity of 1.15, aggregates 10 to 60 μm in length had a specific gravity of 1.06 while aggregates > 60 μm in length had a specific gravity of 1.03. It also was assumed that all organic aggregates were 90% water. Based on regressions developed by Alldredge and Gotschalk (1988), marine snow 0.1 mm in diameter is 60% water while larger particles have a higher water content. Inorganic aggregates were assumed to have a specific gravity of 1.15 and to be 90% water.

Minerals < 10 μm in length were assumed to be spherical while large minerals were assumed to be ellipsoidal, the most commonly encountered shape. Light minerals were assumed to have a specific gravity of 2.5, heavy minerals a specific gravity of 3.5, and opaque minerals a density of 5.00 (personal communication, N. Hawley, Great Lakes Environmental Research Laboratory, NOAA, Ann Arbor). Dry and wet weight densities were assumed to be the same.

Total volume for each phytoplankton species was estimated by summing whole and fragmented cells and then multiplying the number by the average cell volume as provided by E. Stoermer (personal communication, Center for Great Lakes and Aquatic Sciences, The University of Michigan, Ann Arbor).

Phytoplankton were assumed to have a specific gravity of 1.02 (Wetzel 1975) and to be 75% water (Sicko-Goad *et al.* 1984). Zooplankton exoskeletons were assigned an average volume of 1.36×10^6 μm^3, a specific gravity of 1.03 and a dry weight 10% of wet weight.

Mass flux was estimated by converting particle volume to particle wet and then dry weight according to the previously mentioned assumptions of specific gravity and percent dry weight. Daily mass flux on an areal basis was estimated from the mouth area of the trap and the number of days the trap was set. These data were then compared with measured dry weight determinations from the companion freeze-dried chloroform traps. These comparisons allowed for the investigation of the validity of the microscopic reconstruction technique.

Settling Velocities

Settling velocities were estimated in order to identify which particles provided the major transport route of matter through the water column. The settling velocity of particles which are spherical in shape can be estimated by using Stoke's Law: Komar *et al.* (1981) developed modifications of this equation for cylindrical and ellipsoidal particles.

Settling velocities were estimated for mineral particles (assuming a spherical shape for minerals < 10 μm and an ellipsoidal shape for minerals > 10 μm), for fecal pellets (assuming a cylindrical shape), and for fecal matter and organic aggregates (assuming an ellipsoidal shape). Settling velocity was estimated on a particle by particle basis and then the average settling velocity for the various particle types was calculated, e.g., for fecal matter.

Settling velocities were not calculated for phytoplankton because of the complexity of the data sets, i.e., a very large number of species, a variable number of cells within a colony, live versus dead cells, and degrees of fragmentation. Similarly, settling velocities were not estimated for zooplankton exoskeletons.

Data Manipulations

Data were entered on coding sheets and computer programs written to perform the various calculations. There were four output tables. The phytoplankton flux table summarized the condition, i.e., live colony, single cell, < one half a dead cell, of the various taxa identified in the sample and estimated their total volume. Zooplankton exoskeletons also were included in this table. Daily flux rates (wet and dry weight) for each taxonomic category were estimated by converting volume to weight and then estimating flux on the basis of the sediment trap mouth area and the numbers of days the trap was deployed. Total plankton flux also was estimated.

A second table summarized the mean lengths and widths, numbers enumerated and volume of the various categories of mineral particles, aggregates, and zooplankton fecal pellets and fecal matter. A third table, the particle flux table, provided the daily wet and dry weight flux estimates for the minerals, aggregates, zooplankton fecal pellets and fecal matter, and plankton.

RESULTS

Average Particle Sizes

Minerals were dominated by light minerals (55.6% of mineral mass flux) followed by heavy (23.5%) and opaque (20.9%) minerals (Table 1).

TABLE 1. *Mean percent composition (dry weight) of mineral particles based on size and density. L = light, H = heavy and O = opaque.*

Setting Period	< 4 μm			4–10 μm			> 10 μm		
	L	H	O	L	H	O	L	H	O
27 April–17 May	4.0	2.9	0.4	35.6	5.1	4.1	37.6	7.6	2.8
17 May–16 June	5.3	4.7	1.0	16.4	3.4	3.7	46.1	14.7	4.7
16 June–23 July	3.7	5.8	1.7	12.9	10.9	3.9	30.8	18.4	11.7
23 July–17 August	2.0	6.6	0.7	20.4	12.9	9.2	28.9	4.9	14.4
17 August–13 Sept.	4.3	3.2	1.3	7.1	3.4	4.8	26.4	3.7	45.9
13 Sept.–27 Oct.	1.4	9.8	0.9	15.7	12.4	6.6	34.8	10.8	7.8
Mean	3.5	5.5	1.0	18.0	8.0	5.4	34.1	10.0	14.5

TABLE 2. *Mean length (μm) and width (μm) of fecal pellets, fecal matter, organic aggregates, and inorganic aggregates. "Rare" fecal pellets were larger pellets enumerated during the half-filter count. See text for further explanation.*

Setting Period	Fecal pellets		Fecal pellets —large, rare		Fecal matter		Organic aggregates		Inorganic aggregates	
	L	W	L	W	L	W	L	W	L	W
27 April–17 May	22.5	15.2	55.4	25.90	29.1	18.2	15.8	9.1	10.4	6.1
17 May–16 June	37.1	21.7	138.3	39.8	37.0	21.4	20.0	10.8	12.9	6.8
16 June–23 July	36.7	20.7	79.5	30.1	30.5	18.1	17.3	9.5	10.8	7.4
23 July–17 Aug.	32.4	16.2	43.3	24.3	23.7	13.6	20.3	11.0	9.3	6.1
17 Aug.–13 Sept.	28.4	16.4	62.2	33.9	42.6	26.5	31.9	17.1	18.6	9.1
13 Sept.–27 Oct.	22.9	18.4	52.3	29.2	46.3	27.7	43.4	21.3	8.3	5.4
Mean	30.0	18.1	71.5	30.5	34.9	20.9	24.8	13.1	11.7	6.8

Large (> 10 μm) minerals accounted for a greater percentage (58.7%) of total mass flux than small (< 4 μm; 9.9%) and medium (31.4%) size minerals. Overall, large, light minerals comprised the largest component of mineral mass flux averaging 34.1% of the total flux. Although mineral flux varied seasonally and with depth, there were no obvious seasonal nor vertical variations in the composition of this flux.

Most fecal pellets were small with average dimensions of 30.1 μm by 18.1 μm (Table 2). Larger fecal pellets, enumerated primarily during the half-filter count, were rare. Average dimensions of large fecal pellets were 71.5 μm by 30.5 μm. These larger pellets probably were egested by large-bodied adult copepods, i.e., *Diaptomus sicilis* and *Limnocalanus macrurus* (Ferrante and Parker 1977). Very large pellets, as observed in marine studies, were very rare. Thus, the macrozooplankton *Mysis relicta* apparently did not contribute significantly to fecal pellets flux. Fecal matter (average dimensions 34.9 μm × 20.9 μm) was slightly larger than fecal pellets. There were no obvious seasonal nor vertical variations in the size of fecal pellets and matter.

Organic aggregates generally were smaller than fecal pellets and fecal matter (Table 2). Furthermore, unlike fecal pellets and fecal matter, organic aggregates varied seasonally in size (Fig. 1). Aggregates were small from mid-April to mid-August (ca. 20 μm × 10 μm) and then nearly doubled in mean dimension to ca. 43 μm × 21 μm for the September to October trap collections. This seasonal increase in size was associated primarily with organic aggregates in the upper 30 m of the water column: or-

ganic aggregates in deep water (80–95 m) remained similar in size throughout the study period.

Inorganic aggregates did not exhibit any obvious variation in size with depth and season. Length averaged 11.7 μm and width 6.8 μm. Overall, inorganic aggregates tended to be smaller than organic aggregates. This may suggest that as aggregates grow in size, the organic component increases at a greater rate than the inorganic.
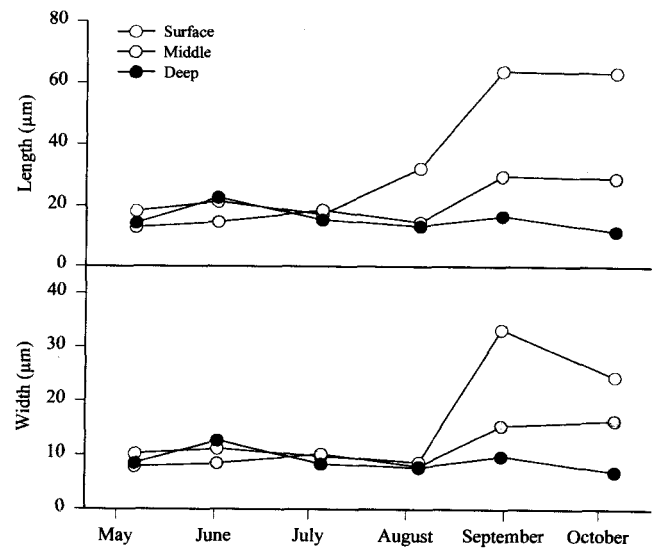

FIG. 1. Seasonal variations in the length and width of organic aggregates in the surface (10 m, 20 m), middle (40 m, 60 m), and deep (80 m, 95 m) sediment traps.

Estimated Versus Measured Dry Weight Particulate Flux

Estimated total dry weight flux (EF) as determined from the mercuric chloride trap series agreed well with measured dry weight determinations (MF) in the chloroform trap series (Figs. 2 and 3). The two estimates were highly correlated indicating that the microscopic reconstruction technique to estimate mass flux was reasonable. Estimated flux was described by:

$$\log(EF) = 1.06\log(MF) - 0.11 \ (r = + 0.94; \ n = 32) \quad (1)$$

While estimated flux was highly correlated with measured flux, EF estimates were slightly lower than MF estimates. Such differences may be partially attributable to the fact that whole zooplankton were excluded from EF calculations but not from MF measurements and calculations: intact zooplankton were not removed from the chloroform trap series prior to weighing. Other differences may be due to underestimates in the specific gravity and weight wet to dry weight conversions of the various particles. Additionally, some of the $CaCO_3$, collected primarily during the August to October period, probably was lost from the $HgCl_2$ poisoned traps. This preservative lowers the pH of the sample
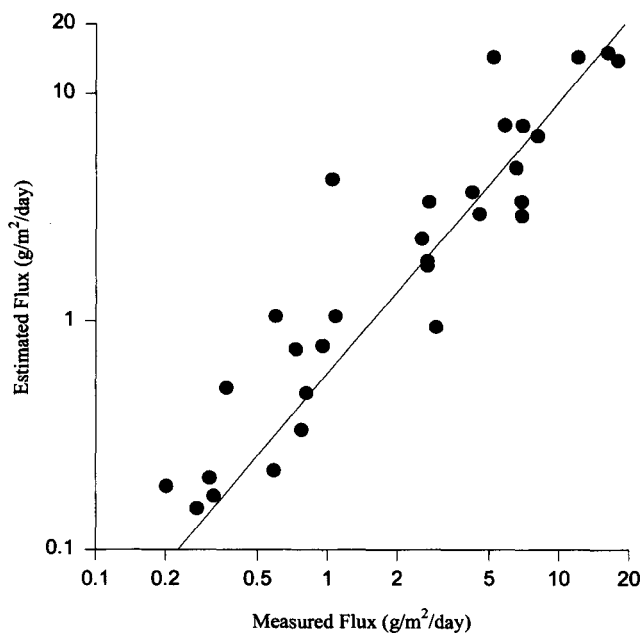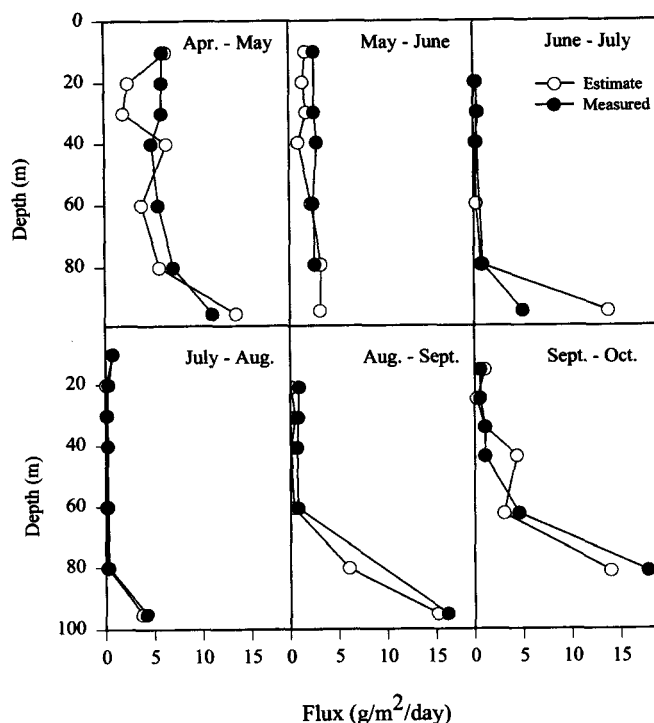

FIG. 3. *Estimated versus measured versus dry weight flux, by setting and depth. The 10- m traps were not successfully recovered for the June to July and August to September settings: nor were the 95-m traps for the September–October setting successfully recovered.*

inducing dissolution of the $CaCO_3$, although incorporation into organic aggregates should retard dissolution and calcite crystals were observed microscopically.

Seasonal Variations in Estimated Dry Weight Flux

Estimated fluxes varied seasonally and with depth (Fig. 3); the overall pattern of mass fluxes was consistent with the 15-year record from this site (Eadie 1997). Fluxes over 26 April to 17 May averaged 5.4 g/m^2/day in the upper 80 m of the water column, increasing to 14.4 g/m^2/day at 95 m. Particulate flux was dominated by zooplankton egestion products with fecal pellets and fecal matter accounting for an average of 5.6% and 36.8% respectively of total mass flux (Fig. 4). Fecal pellets were an especially significant component (22.9%) of flux at 30 m. Minerals were the next largest component of flux (water column average 19.4%), accounting for 21 to 34% of mass flux at 60–95 m.

Measured versus Estimated Flux

FIG. 2. *Estimated versus measured dry weight flux.*

Phytoplankton accounted for an average of only 12.7% of mass flux with the diatoms *Melosira* and *Stephanodiscus* dominating. Many algal cells were dead and fragmented suggesting intense zooplankton grazing. Organic aggregates (12.0%) and zooplankton exoskeletons (11.1%) accounted for most of the remainder of the flux. Inorganic aggregates were minor components of flux in April–May and in the succeeding months.

Estimated fluxes decreased over 17 May to 16 June (Fig. 3) with lake warming and increased stabilization of the water column. In contrast to the April–May setting, fluxes were relatively uniform with depth, averaging 2.1 g/m²/day. Particulate flux was even more strongly dominated by fecal pellets (water column average 16.3%) and fecal matter (37.6%) than during the previous setting (Fig. 4). Phytoplankton were the next largest component of flux (16.3%) with the diatoms *Melosira* and *Stephanodiscus* the predominate taxa. Organic aggregates were minor components of flux (water column average 14.5%) except at 20 m where they accounted for an average of 39.5% of flux: organic aggregates in this sample were difficult to distinguish from fecal matter. Minerals (13.1%) were a

smaller component of flux than in the preceding month. Zooplankton exoskeletons were observed only at 80 m.

With the exception of the 95 m setting, estimated fluxes declined further over 16 June to 23 July (Fig. 3). Estimated fluxes averaged only 0.38 g/m²/day between 20 and 80 m: the 10 m traps were not recovered successfully during this setting. Flux increased markedly at 95 m (14.5 g/m²/day), indicating that there was a well-developed nepheloid layer. Fecal pellets and fecal matter continued to be major contributors to flux accounting for water column averages of 8.5% and 22.6% respectively: the greatest contributions were at 40 and 60 m (Fig. 4). Organic aggregates were a major component of flux at 20 m (17.1%) and 30 m (22.0%). Phytoplankton accounted for an average of 21.9% flux with the greatest percentage contribution at 40 to 80 m. Phytoplankton were dominated by the diatoms *Melosira* and *Tabellaria*. Minerals were a minor component of flux except at 95 m where they accounted for 77.9% of total flux. Zooplankton exoskeletons were major components of flux at 20 m (32.3%), 30 m (15.9 %), and 80 m (30.9%).
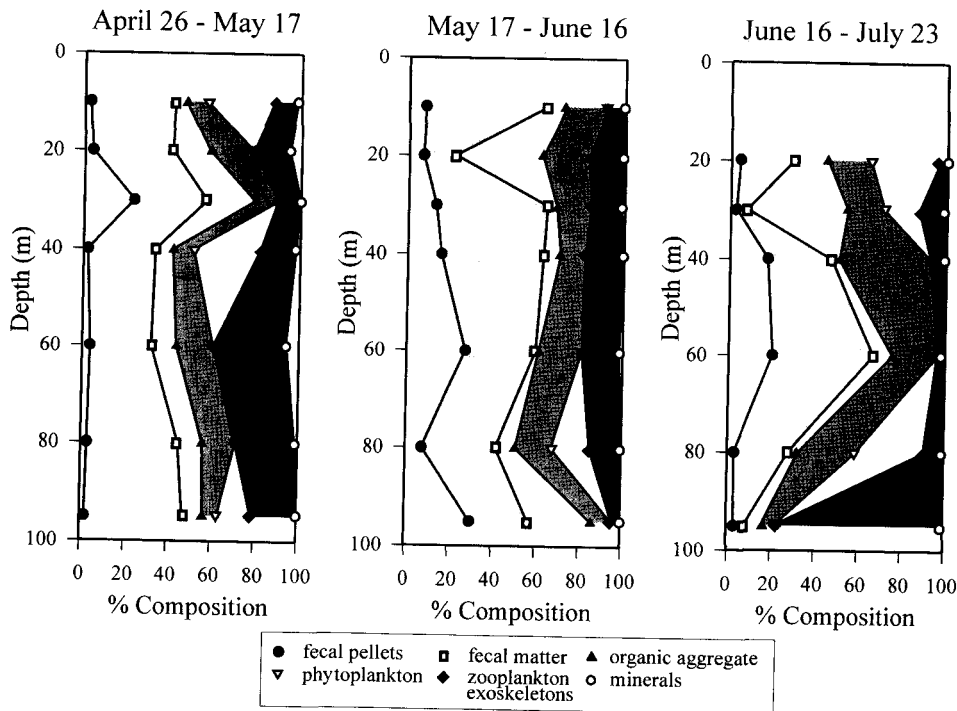
Fluxes remained low over the 23 July to 17 Au-

FIG. 4. *Percent composition by month and depth of particles comprising dry weight flux. April to July trap settings.*
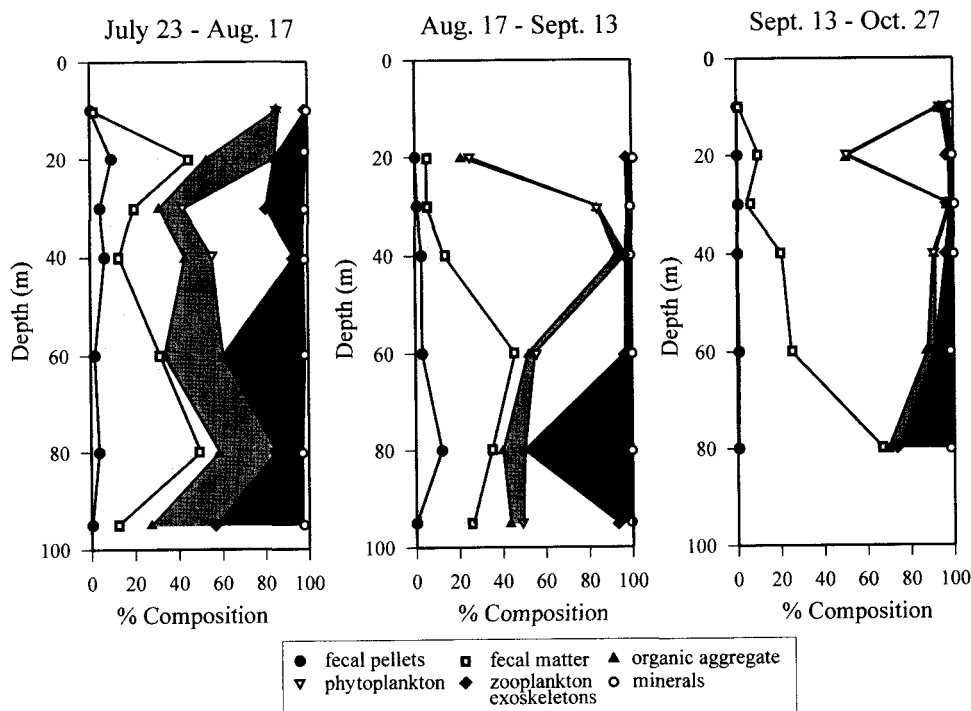
FIG. 5. Percent composition by month and depth of particles comprising dry weight flux. July to October trap settings.

gust setting averaging 0.2 g/m²/day in the upper 80 m of the water column and 3.8 g/m²/day at 95 m (Fig. 3). This period typically is one of strong vertical stratification, relatively low phytoplankton stocks in the upper regions of the water column, and a period in which zooplankton experience significant food limitation. A deep chlorophyll layer, generally dominated by diatoms, resides below the thermocline (Brooks and Torke 1977).

Fecal pellets accounted for an average of 3.8% of July to August mass flux while fecal matter accounted for an average of 20.9% of flux (Fig. 5). Organic aggregates were considerably more prevalent than in the earlier months accounting for 85.4% of the mass flux at 10 m and 30.0% at 40 m: the water column average was 23.1%. Phytoplankton accounted for an average of 0.3% of total flux at 10 m, 31.6% at 20 m, and then 10.8 to 29.4% at greater depths. Zooplankton exoskeletons were a large component of flux at 30 m and 40 m (38.1%). Minerals accounted for 17.2% of the flux at 30 m: this strong contribution was due to two large (ca. 21 µm × 20 µm) light and two large (ca. 48 µm × 14 µm) opaque minerals encountered on the microscope slide. Presumably these minerals had atmospheric

sources. Minerals also were important at 60 m (38.0%) and 95 (40.1%) m.

Fluxes increased over 17 August to 13 September (Fig. 3) with the onset of lake cooling, especially at 80 m (6.0 g/m²/day) and 95 m (15.1 g/m²/day). Estimated rates averaged 0.2 g/m²/day between 20 and 60 m: the 10 m traps were not successfully recovered. Particulate flux in the upper 40 m of the water column was dominated by organic aggregates with substantially smaller contributions by fecal matter, phytoplankton, and zooplankton exoskeletons (Fig. 5). Fecal matter (30.7%) dominated in deeper waters followed by zooplankton exoskeletons (28.2%) and minerals (19.5%): organic aggregates (9.4%), phytoplankton (6.9%) and fecal pellets (5.0%) were minor contributors of flux in deeper waters. This is the period of high measured CaCO₃ from authogenic whitings (Strong and Eadie 1978).

Fluxes increased over 13 September to 27 October (Fig. 3) averaging 1.9 g/m²/day in the upper 60 m of the water column and 14.0 g/m²/day at 80 m: the 95 m traps were not successfully recovered. Organic aggregates were the dominant component of flux (71.5%) at all depths except 80 m (Fig. 5). Fecal matter was the second largest component (21.0%) of mass flux with this contribution increas-
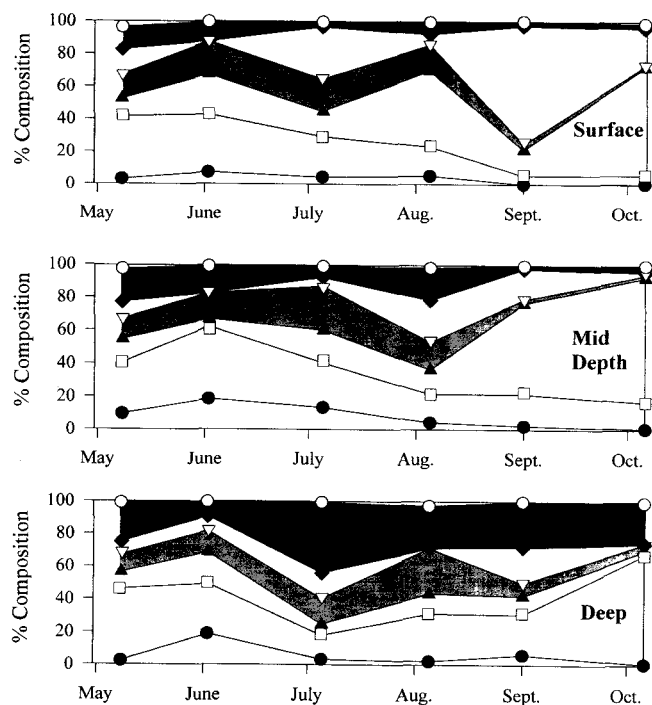
FIG. 6. Seasonal variations in the composition of mass flux by depth zone.

ing with depth. Zooplankton exoskeletons were a major component of flux at 30 m (46.4%) with a lesser contribution at 40 m (4.8%). Minerals were a minor component of flux with this contribution increasing with depth.

For the purpose of summarizing seasonal and vertical trends in mass flux, the water column was divided into three depth regions, i.e., surface (10 to 20 m), middle (30 to 60 m), and deep (80 to 95 m) waters (Fig. 6). In the upper, productive region of the water column, fecal pellets and fecal matter accounted for more than 40% of mass flux during spring (Fig. 6). Zooplankton egestion products accounted for less of the mass flux through summer as food became limiting: organic aggregates became increasingly more important at these times. Zooplankton exoskeletons were important in late spring–early summer and late summer–early autumn. Mineral particles and phytoplankton were minor components of surface flux in most months.

As in surface waters, fecal pellets and fecal matter were the major components of flux at mid-depths during spring and early summer (Fig. 6). However, fecal pellets provided a stronger contribu-

tion to mid-depth than surface flux. This larger contribution may, in part, be related to the fact that copepods, especially calanoids, dominate the hypolimnetic zooplankton community; calanoid copepods produce discrete fecal pellets. Cladocerans, cyclopoids, and immature calanoid copepods, including nauplii, tend to predominate in surface waters (Wells 1960, Evans unpublished data) and produce less discrete fecal pellets. Organic aggregates were minor components of flux in spring but were of major importance in late summer and early autumn. Minerals generally were a minor component of flux except in July. Phytoplankton was of some importance in spring while zooplankton exoskeletons were more important in summer. Zooplankton exoskeletons accounted for less of the flux at mid-depths than in surface waters.

Flux in the deepest region of the water column (80 and 95 m) generally was dominated by fecal pellets and fecal matter (Fig. 6) with fecal matter predominating. Minerals also were important. Their greater contribution in deep than in surface and mid-depth waters suggests that resuspension was an important source of these materials. Phytoplankton were also a significant contributor to flux: some cells may have been resuspended from the lake floor. Organic aggregates were minor components of flux as were zooplankton exoskeletons.

Estimated Settling Velocities

There were large variations in the estimated mean settling velocity of mineral particles ranging from 0.5 m/day for small (< 4 μm), light minerals to 12.9 m/day for large (> 10 μm) opaque minerals (Table 3). Some of the larger, opaque minerals had estimated individual settling rates of more than 30 m/day. Given these high settling rates, these larger minerals probably originated from dry deposition (i.e., the atmosphere) rather than resuspension from

TABLE 3. Estimated mean settling velocity (m/day) on minerals by size and density. Means are averaged across all six setting periods and seven depths.

Density	Size Categories		
	< 4 μm	4–10 μm	> 10 μm
Light	0.45	3.05	8.43
Heavy	0.76	5.09	9.74
Opaque	1.27	8.11	12.87

the lake floor. Mean estimated residence time between 10 m and 100 m was 7 days for a large, opaque mineral and 180 days for a small, light mineral.

Mean settling velocities of fecal pellets averaged 5.4 m/day (Table 4) providing a theoretical residence time of 16.7 days between 10 and 100 m. These estimates compare favorably with Ferrante and Parker's (1977) estimate of an average sinking velocity of 4.4 m/day for Lake Michigan copepod fecal pellets. Larger, rare fecal pellets had considerably faster settling rates averaging 19.8 m/day. This provided a theoretical residence time of 4.6 days between the epilimnion and lake floor.

Fecal matter had lower estimated settling velocities than fecal pellets averaging 3.2 m/day versus 5.4 m/day (Table 4). Differences between the two settling rates were due to the fact that fecal pellets had a lower assumed specific gravity than fecal matter; there were only minor differences in the mean lengths and widths of the two classes of particles. There were no obvious seasonal variations in fecal matter settling velocities. Fecal matter had an average theoretical residence time of 27.9 days between the epilimnion and 100 m.

Organic aggregates had an estimated mean settling velocity of 1.5 m/day (Table 4), providing a theoretical residence time of 62.1 days between the epilimnion and the lake floor. These estimates compare favorably with Burns and Rosa's (1980) *in situ* estimates of 0.24 m/day for aggregates 1 to 10 μm in size to 2.32 m/day for aggregates > 64 μm in size. Estimated settling velocities exhibited a strong seasonal pattern increasing from a low mean value of 0.5 m/day (corresponding to a 180 day residence time between 10 and 100 m) in April to May to a maximum water column average of 3.6 m/day (25.1 day residence time between 10 and 100 m) in September–October. This seasonal pattern was associated with a seasonal increase in the size of organic aggregates, primarily in the upper water column (Table 2, Fig. 2).

Phytoplankton settling velocities were not estimated in this study but were likely to be low when compared to minerals, fecal pellets, fecal matter, and organic aggregates. Living cells typically have settling rates of < 2 m/day (Wetzel 1975). Burns and Rosa (1980) measured *in situ* phytoplankton settling velocities of 0.08 to 0.31 m/day. Dead but otherwise intact cells may have similar settling rates as living algal cells. Fragmented cells were comprised mainly of diatoms. While diatom frustules are composed largely of silicon (i.e., a "light" mineral), settling rates would have been lower than that estimated for light minerals. This is because frustules have various pores (striae, aerolae, punctae) which would serve to reduce specific gravity. In addition, fragments were plate-like, rather than spherical, and this also would have operated to reduce settling velocity. As previously noted, zooplankton exoskeleton settling velocities were not estimated because of their complex geometry. It is probable that they settle slowly and are subject to considerable decay before reaching the lake floor.

DISCUSSION

Particulate flux studies have tended to assume different emphases, depending on where they were conducted. Marine studies generally have been conducted in offshore waters where flux is comprised primarily of biological material of autochthonous origin: clays and silts of lithogenic origin tend to become associated within autochthonous material (Honjo 1982). Sediment trap placement often has been below the permanent thermocline and frequently at very great depths. In such studies, flux tends to be dominated by highly refractile material,

TABLE 4. Estimated mean settling velocities (m/day), by setting period, of fecal pellets, fecal matter, organic aggregates, and inorganic aggregates. See text for further explanation.

Setting Period	Fecal pellets	Fecal pellets —large, rare	Fecal matter	Organic aggregates	Inorganic aggregates
27 April–17 May	4.57	10.98	2.29	0.45	0.26
17 May–16 June	6.05	28.24	3.02	0.60	0.37
16 June–23 July	7.53	16.01	2.29	0.63	0.51
23 July–17 Aug.	5.15	9.77	2.26	1.20	0.46
17 Aug.–13 Sept.	4.51	39.91	5.24	2.20	0.70
13 Sept.–27 Oct.	4.53	13.81	4.27	3.59	0.11
Mean	5.39	19.79	3.23	1.45	0.40

which settles slowly without degradation, and rapidly-sinking biological material, which does not remain in the productive upper layers long enough to be degraded (or consumed). As a consequence, microscopic studies of flux composition have focused on the importance of large, rapidly-sinking fecal pellets and fecal matter in transporting material to the ocean floor (Bishop *et al.* 1977, Higgo *et al.* 1977). Other research has focused on the composition, physical attributes and formation of marine snow, i.e., large (2.4 to 75 mm in size) aggregates with rapid sinking rates (Alldredge and Gotschalk 1988). Such studies have focused on the upper 100 m of the water column, possibly because aggregate abundance decreases markedly below the euphotic zone (Gordon 1970).

Marine studies, conducted in coastal bays, have had a slightly different focus than oceanic studies. This difference probably related to three factors. First, coastal systems are shallower and, as such, seasonally rather than permanently stratified. Second, seasonality in production is more dramatic than in the less productive offshore waters. Third, terrestrial organic and lithogenic inputs may be significant. Fecal pellets have been shown to be important in particulate flux transport, although this importance varies seasonally (Taguchi and Hargrave 1978, Prahl and Carpenter 1979). Greater emphasis in these studies has been given to the role of stratification in affecting seasonality in fluxes (Hargrave and Taguchi 1978). Fluxes tend to be highest during periods of low stratification: resuspension has been implicated as the primary factor affecting these high rates. During stratification, flux is more strongly linked to primary production and zooplankton biomass.

Particulate flux in the offshore waters of lakes Michigan and Ontario have been shown to vary seasonally, being highest during periods of vertical mixing (Chambers and Eadie 1981, Bloesch 1982, Schelske *et al.* 1984, Eadie *et al.* 1984). These high rates have been related to the resuspension of fine-grained material which is transported from the inshore to the offshore. However, the role of zooplankton in this particulate transport is poorly understood. Are zooplankton important in the "fecal pellet express" of material from the euphotic zone to the sediments as has been observed in deep oceanic waters? Or do zooplankton have a minor role, except during stratification, with spring and autumn flux more strongly dominated by resuspended lithogenic particles?

Source and Composition of Particulate Flux

Particulate flux in this study was dominated by biological matter with matter of autochthonous origin predominating during the entire April to October study period: obvious terrestrial matter such as pollen, insect parts, and tree leaf fragments were exceedingly rare. Minerals accounted for an average of only 15.2% of mass flux. Moreover, although flux varied from a water column high of 6.1 $g/m^2/day$ over April to May to a low of 0.7 $g/m^2/day$ over July to August, there were relatively small variations in the mineral contribution to flux. Minerals accounted for an average of only 18.6% of the April to May flux and 14.8% of the May to June flux. This suggests that the contribution of mineral flux to total flux was relatively independent of vertical mixing. In contrast, there was substantial seasonal variation in the percentage contribution of organic aggregates, phytoplankton and, to a lesser extent, fecal pellets in flux.

Mineral flux was dominated by silt-sized particles. These particles had several potential sources: resuspension from the sediments, lateral transport along the lake floor, riverine inputs, atmospheric inputs, and *in situ* production through calcium carbonate precipitation (Strong and Eadie 1978). Based only on estimated sedimentation rate, silts required many days to sink from 10 m to the 100 m deep lake floor: 7 days for a large silt particle settling at 12.9 m/day, 16.7 days for a silt particle settling at 5.4 m/day, and 90 days for a silt particle settling at 1 m/day.

During strong vertical mixing, silts may be rapidly transported back to the surface or at an accelerated rate toward the lake floor. But strong vertical mixing keeps these silt particles in suspension, essentially preventing them from settling onto the lake floor and becoming incorporated into the sediments. During this time, when silt particles are kept in suspension by strong, vertical mixing, they may be ingested by zooplankton, adsorbed onto fecal matter, or incorporated into organic aggregates. In addition, sedimenting silts may be transported laterally. A silt particle settling through water with a horizontal current velocity of 6 cm/sec theoretically is transported 5.2 km horizontally over a 24 hour period. An individual silt mineral sedimenting at 0.5 to 12.9 m/day could travel tens to hundreds of kilometers before reaching the lake floor. Thus, silts entering the sediment traps in this study could have originated from several sources. The relative importance of lateral transport can be inferred from mea-

surement of ^{137}Cs inventories in cores and calculation of sediment focusing factors (Robbins 1978, Robbins *et al.* 1978, Edgington and Robbins 1990).

Particulate flux was dominated by biological matter of autochthonous origin, even during periods of strong vertical mixing. Most particles had slow, estimated mean settling rates: 5.6 m/day for fecal pellets, 3.2 m/day for fecal matter, and only 1.5 m/day for organic aggregates, i.e., in the same range as estimated for the smaller silt-sized mineral particles dominating mineral flux. Large fecal pellets were rare and had slow settling rates (mean 19.8 m/day) when compared to marine studies. This slowly settling biological matter had the same propensity as silt-sized minerals to be kept in suspension during periods of strong vertical mixing and in regions of the water column where turbulence was significant, i.e., the epilimnion and metalimnion. There also was a strong potential for significant lateral transport. The offshore movement of the thermal bar is a well-known phenomenon in Lake Michigan, with warmer, turbid water migrating offshore with spring warming into the colder, clearer offshore waters. There must also be a significant offshore transport of fecal pellets, fecal matter, phytoplankton, and other biological material with the migrating thermal bar.

Biological particles undergo significant transformations while settling through the water column. Copepod fecal pellet membranes may break down in as little as 6 to 14 days (Ferrante and Parker 1977) and their contents dispersed into the water shortly thereafter: degradation occurs more rapidly at warm than cold temperatures. Fecal matter and the organic materials cementing aggregates together also degrade (Meyers and Eadie 1993) significantly on these time scales. With degradation into smaller particles, settling velocities diminish. Zooplankton exoskeletons and dead and fragmented phytoplankton also are degraded while settling though the water column although less is known about these processes. This *in situ* degradation of organic-based substrate supports the hypothesis proposed to explain the observation of recycling of hydrophobic organic compounds in Lake Superior (Baker *et al.* 1991).

Biological particles may be repackaged while settling through the water column. Fecal pellets and fecal matter may be ingested (Paffenhofer and Knowles 1979), particularly when they are within the zooplankton preferred size range. In general, most freshwater zooplankton feed on particles < 40 μm in length (Vanderploeg *et al.* 1987) although many feed preferentially on smaller particles. Mean

fecal pellet and fecal matter lengths were 30.0 μm and 34.9 μm, respectively, i.e., within the feeding range of most adult copepods. Dead and fragmented settling phytoplankton also may be ingested. Alternately, they may become attached to and bound within organic inorganic aggregates.

Lake Michigan is thermally stratified for approximately half of the year. Offshore waters generally are stratified strongly from late June to August with the thermocline beginning to deepen in September and breaking down by December. Vertical mixing is intense during winter, except during periods of ice cover. As a consequence of this intense vertical mixing, the physical environment operates to keep slowly settling particles in suspension for much of the year. Fecal pellets and matter, because they settle slowly in this physically dynamic environment, must stay in suspension for relatively long periods of time during which they must follow several pathways before their individual components reach the lake floor: downward and upward movement, lateral transport, degradation and disintegration, ingestion, adsorption onto organic aggregates, etc.

Fecal pellets produced during thermal stratification also apparently followed several pathways before reaching the lake floor. Fecal pellets and fecal matter obtained from the July to September trap settings were small and settled at slow rates. Moreover, slow-settling organic aggregates became increasingly more important in the upper regions of the water column, possibly because intense zooplankton grazing reduced the contribution of fecal pellets and fecal matter to flux. In oligotrophic lakes such as Michigan, the summer and the early autumn months are a period of food limitation for most zooplankton. While there is a deep-chlorophyll layer during summer months, this is generally most available to lower metalimnetic and hypolimnetic zooplankton such as *Limnocalanus macrurus* and *Diaptomus sicilis* and to macrozooplankton such as *Mysis relicta*. In addition, cladocerans, with their diffuse egestion products, become more abundant in the upper regions of the water column. These taxa are especially efficient at grazing smaller particles and may have had a major role in the low numbers of small fecal pellets, fecal matter, and organic aggregates observed in the upper sediment trap.

In surface waters, fecal pellets and fecal matter were the major contributors to mass flux only from April to July: after that, intense grazing by the food-limited zooplankton community efficiently retained organic matter in the euphotic zone. At mid-

depths, fecal pellets and fecal matter were the major contributors to mass flux in all months but August to September. In deep water, fecal pellets and matter were the major contributors to mass flux. This is similar to results obtained in oceanic studies which have emphasized the importance of fecal pellets in the transport of matter from the euphotic zone to greater ocean depths. However, although zooplankton fecal pellets and fecal matter were the major contributors to mass flux, they did not always travel rapidly to the sediments. As a consequence of their slow settling rate, the contents of fecal pellets and fecal matter undoubtedly traveled along several pathways before reaching the lake sediments, particularly during periods of intense vertical mixing.

The absence of large, mysid fecal pellets in the sediment traps was puzzling. It is possible that mysid fecal pellets were collected by the sediment traps but not sampled adequately in the laboratory, i.e., they settled rapidly when the sample bottle was gently resuspended for subsampling. However, it is more probable that mysids were not of sufficient abundance to produce large numbers of fecal pellets. Moreover, vertically migrating mysids may have retained food ingested in the surface layers in their gut, digesting and later egesting fecal pellets after they had returned to the lake floor.

The results of this study suggest that changes in zooplankton community structure should affect not only grazing pressure on the phytoplankton assemblage but also the pathways followed by sedimenting autochthonous matter toward the lake floor. A shift toward large-bodied copepods, especially calanoid copepods, should be accompanied by the increased production of relatively rapidly sinking fecal pellets. However, a shift toward a cyclopoid and cladoceran community should result in a shift toward smaller, easily fragmented fecal pellets and diffuse egestion products with relatively slow sinking rates. Organic matter should be retained and recycled more efficiently in a water column dominated by cladocerans and cyclopoid copepods than a water column dominated by calanoid copepods.

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REFERENCES

Alldredge, A. L., and Gotschalk, C. 1988. In situ settling velocity of marine snow. *Limnol. Oceanogr.* 33:339–351.

Ansell, A. D. 1974. Sedimentation of organic detritus in Locks Etive and Creran, Argyll, Scotland. *Mar. Biol.* 27:263–273.

Baker, J. E., Eisenreich, S. J., and Eadie, B. J. 1991. Sediment trap fluxes and benthic recycling of organic carbon, PAH and PCB congeners in Lake Superior. *Environ. Sci. Technol.* 25:500–509

Bishop, J. K. B., and Marra, J. 1984. Variations in primary production and particulate carbon flux through the base of the euphotic zone at the site of the Sediment Trap Intercomparison Experiment (Panama Basin). *J. Mar. Res.* 42:189–206.

———, Edmond, J. M., Ketten, D. R., Bacon, M. P. and Silker, W. B. 1977. The chemistry, biology, and vertical flux of particulate matter from the upper 400 m of the equatorial Atlantic Ocean. *Deep-Sea Res.* 24:511–548.

Bloesch, J. 1982. Inshore-offshore sedimentation differences resulting from resuspension in the eastern basin of Lake Erie. *Can. J. Fish. Aquat. Sci.* 39:748–759.

Brooks, A. S., and Torke, B. G. 1977. Vertical and seasonal distribution of chlorophyll *a* in Lake Michigan. *J. Fish. Res. Board can.* 34:2280–2287.

Burns, N. M., and Rosa, F. 1980. In situ measurements of the settling velocity of organic carbon particles and 10 species of phytoplankton. *Limnol. Oceanogr.* 25:855–864.

Chambers, R. L., and Eadie, B. J. 1981. Nepheloid and suspended particulate matter in southeastern Lake Michigan. *Sedimentology* 28 439–447.

Chase, R. L. 1979. Settling behavior of natural aquatic particles. *Limnol. Oceanogr.* 24:417–425.

Deuser, W. G., Ross, E. H., and Anderson, R. F. 1981. Seasonality in the supply of sediment to the deep Sargasso Sea and implications for the rapid transfer of matter to the deep ocean. *Deep-Sea Res.* 28A:495–505.

Eadie, B.J. 1997. Probing particle processes in Lake Michigan using sediment traps. *Water, Air, and Soil Pollution* 99:133–139.

————, Chambers, R. L., Gardner, W. S., and Bell, G. L. 1984. Sediment trap fluxes in Lake Michigan: resuspension and chemical fluxes in the southern basin. *J. Great Lakes Res.* 10:307–322.

————, Vanderploeg, H. A., Robbins J. A., and Bell, G. L. 1989. The significance of sediment resuspension and particle settling. In *Large Lakes: Ecological Structure and Function*, eds. M. M. Tilzer and C. Serruya, pp. 196–209. Springer Verlag.

Edgington, D. N., and Robbins, J. A. 1990. Time scales of sediment focusing in large lakes as revealed by measurement of fallout of Cs-137. In *Large Lakes: Ecological Structure and Function*, eds. M. M. Tilzer and C. Serruya. pp. 210–223. Springer Verlag.

Elder, D. L., and Fowler, S. W. 1977. Polychlorinated biphenyls: penetration into the deep ocean by fecal pellets. *Science* 197:459–461.

Ferrante, J. G., and Parker, J. I. 1977. Transport of diatom frustules by copepod fecal pellets to the sediments of Lake Michigan. *Limnol. Oceanogr.* 22:92–98.

Gardner, W. S., Eadie, B. J., Chandler, J. F., Parrish, C. C., and Malczyk, J. M. 1989. Mass flux and nutritional composition of settling epilimnetic particles in Lake Michigan. *Can. J. Fish. Aquat. Sci* 46: 1118–1124

Glover, R. M. 1982. Diatom fragmentation in Grand Traverse Bay, Lake Michigan and its implications for silica cycling. Ph. D. thesis, Dept. of Oceanic Science, The University of Michigan. Ann Arbor, Michigan.

————, and Evans, M. S. 1981. The composition of particles in Lake Michigan using S.E.M. and light microscope techniques. *Micron* 12:297–298.

Gordon, D. C. Jr. 1970. A microscopic study of organic particles in the North Atlantic Ocean. *Deep-Sea Res.* 17:175–185.

Hargrave, B. T., and Taguchi, S. 1978. Origin of deposited material sedimented in a marine bay. *J. Fish. Res. Board Can.* 35:1604–1613.

Higgo, J. J. W., Cherry, R. D., Hegraud, M., and Fowler, S. W. 1977. Rapid removal of plutonium from the oceanic surface layer by zooplankton fecal pellets. *Nature* 266:623–624.

Honjo, S. 1982. Seasonality and interaction of biogenic and lithogenic particulate flux at the Panama Basin. *Science* 218:883–884.

————, Spencer, D. W., and Farrington, J. W. 1982. Deep advective transport of lithogenic particles in the Panama Basin. *Science* 216:516–518.

Komar, P. D., Morse, A. P., Small, L. F., and Fowler, S. W. 1981. An analysis of sinking rates of natural copepod and euphausid fecal pellets. *Limnol. Oceanogr.* 26:172–180.

McCave, I. N. 1975. Vertical fluxes of particles in the ocean. *Deep Sea Res.* 22:491–502.

Meyers, P. A., and Eadie, B. J. 1993. Sources, degradation and recycling of organic matter associated with

sinking particles in Lake Michigan. *Org. Geochem.* 20:47–56

Oviatt, C. A., and Nixon, S. A. 1975. Sediment resuspension and deposition in Narragansett Bay. *Est. Coastal Mar. Science* 3:201–207.

Paffenhofer, G. A., and Knowles, S. C. 1979. Ecological implications of fecal pellet size, production and consumption by copepods. *J. Mar. Res.* 37:35–49.

Prahl, F. G., and Carpenter, R. 1979. The role of zooplankton fecal pellets in the sedimentation of polycyclic aromatic hydrocarbons in Dabab Bay, Washington. *Geochem. et Cosmochim. Acta* 43: 1959–1972.

Robbins, J. A. 1978. Geochemical and geophysical applications of radioactive lead. In *The Biogeochemistry of Lead in the Environment*, ed. J. O. Nriagu, pp. 285–393. New York: Elsevier/North-Holland Biomedical Press.

————, and Eadie, B. J. 1991. Seasonal cycling of trace elements, Cs-137, Be-7 and Pu-239+240 in Lake Michigan. J. *Geophys. Res.* 96:17081–17104.

————, Edgington, D. N., and Kemp, A. l. W. 1978. Comparative ^{210} Pb and ^{137} Cs, and pollen chronologies of sediments from lakes Ontario and Erie. *Quat. Res.* 10:256–278.

Rosa, F. 1985. Sedimentation and sediment resuspension in Lake Ontario. *J. Great Lakes Res.* 11:13–25.

Schelske, C. L., Eadie, B. J., and Krausse, G. L. 1984. Measured and predicted fluxes of biogenic silica in Lake Michigan. *Limnol. Oceanogr.* 29:99–110.

Sicko-Goad, L. M., Schelske, C. L., and Stoermer, E. F. 1984. Estimation of intracellular carbon and silica content of diatoms from natural assemblages using morphometric techniques. *Limnol. Oceanogr.* 29:1170–1178.

Strong, A., and Eadie, B. J. 1978. Satellite observations of calcium carbonate precipitation in the Great Lakes. *Limnol. Oceanogr.* 23:877–887

Taguchi, S., and Hargrave, B. T. 1978. Loss rates of suspended material sedimented in a marine bay. *J. Fish. Res. Board Can.* 35:1614–1620.

Vanderploeg, H.A., Eadie, B. J., Liebig, J. R., Tarapchak, S. J., and Glover, R. M. 1987. Contribution of calcite to the particle-size spectrum of Lake Michigan seston and its interactions with the plankton. *Can. J. Fish. Aquat. Sci.* 44: 1898–1914

Webster, T. J. M., Paranjape, M. A., and Mann, K. H. 1975. Sedimentation of organic matter in St. Margaret's Bay, Nova Scotia. *J. Fish. Res. Board Can.* 32:1399–1407.

Wells, L. 1960. Seasonal abundance and vertical movements of planktonic Crustacea in Lake Michigan. *Fish. Bull.* 60:343–364.

Wetzel, R. G. 1975. *Limnology.* 1st Ed. Philadelphia: W. B. Saunders. Co.